

## A new biogeographically disjunct giant gecko (*Gehyra*: Gekkonidae: Reptilia) from the East Melanesian Islands

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### Abstract

The East Melanesian Islands have been a focal area for research into island biogeography and community ecology. However, previously undescribed and biogeographically significant new species endemic to this region continue to be discovered. Here we describe a phylogenetically distinct (~20% divergence at the mitochondrial ND2 gene) and biogeographically disjunct new species of gecko in the genus *Gehyra*, from the Admiralty and St Matthias Islands. *Gehyra rohan* sp. nov. can be distinguished from all congeners by the combination of its very large size, ring of bright orange scales around the eye, moderate degree of lateral folding on the limbs and body, and aspects of head, body and tail scutellation. Molecular data indicate mid to late Miocene divergence of the new species from nearest relatives occurring nearly 2000 kilometres away in Vanuatu and Fiji. Large *Gehyra* have not been recorded on the intervening large islands of the Bismarck Archipelago (New Britain and New Ireland) and the Solomon Islands, suggesting this dispersal pre-dated the current configuration of these islands, extinction in intervening regions, or potentially elements of both. Conversely, low genetic divergence between disjunct samples on Manus and Mussau implies recent overseas dispersal via either natural or anthropogenic means.

**Key words:** Admiralty Islands, endemism, Fiji, Manus, Miocene, Mussau, molecular dating, overwater dispersal, Vanuatu

### Introduction

The islands of Melanesia, comprising the large landmass of New Guinea and numerous smaller islands to the north and east, formed at the intersection of the Australian and Pacific plates and have had a complex and dynamic geological history (Ewart 1988; Hall 2002; Polhemus 2007; Davies *et al.* 2012). The East Melanesian Islands include - from west to east - the Admiralty Islands, New Britain, New Ireland, the Solomons, and in some interpretations Vanuatu and Fiji (Lucky & Sarnat 2010). These islands have also been referred to as Northern Melanesia (Mayr & Diamond 2001). All of these major island systems have at least some endemic vertebrate taxa, and molecular analyses increasingly show that some of these endemics are genetically highly divergent (Cleere *et al.* 2007; Skinner *et al.* 2011; Strickland *et al.* 2016). However, the origins of the majority of East Melanesian endemics remain untested using modern molecular phylogenetic methods. Key questions yet to be comprehensively addressed are: how long have endemic terrestrial lineages been present in insular East Melanesia (in particular: do any have origins dating back to the island arcs that may have formed in the region as long ago as the Oligocene or late Miocene (Hall 2002)); from where did these endemic species originate, and what has been the

nature and timing of dispersal between the islands? A further complication to resolving the biogeographic history and affinities of this region is that distinct and divergent new taxa continue to be discovered (Weijola *et al.* 2016; Timm *et al.* 2016).

The Admiralty Islands are the western-most islands of East Melanesia, positioned nearly 300 kilometres north of New Guinea, and a similar distance west of New Ireland and New Hanover (Mayr & Diamond 2001). The largest island in this group, Manus, is a composite of volcanic and limestone substrates and may have been subaerial since the late Miocene (nearly 8–10 million years ago) (Thompson 1952), although other work suggests more recent exposure (Davies *et al.* 2012). The St. Matthias Islands (of which the largest is Mussau) lie approximately 300 km to the east of the Admiralty Islands and are smaller, but comprise a similar composite of a central volcanic spine with fringing limestones (Kirch & Catterall 2001). There is considerable endemism in birds, mammals, reptiles and frogs on both Manus and Mussau (Zug & Fisher 2012; Richards *et al.* 2014; Whitmore *et al.* 2015; Weijola *et al.* 2016).

*Gehyra* is one of the most diverse Australasian gecko radiations, with over 40 recognised species (and many more awaiting description) distributed across Southeast Asia, Australia, and Melanesia. In contrast with some other gekkonid radiations occurring in Melanesia (Oliver *et al.* 2012), but like many trans-Wallacean radiations, diversity in this group is asymmetrically distributed — it is most speciose in Australia (Heinicke *et al.* 2011; Doughty *et al.* 2012; Sistrom *et al.* 2013; Oliver *et al.* 2016), with a subsidiary centre of endemism in New Guinea (Oliver *et al.* 2010, Skipwith & Oliver 2014). The recognized species diversity of *Gehyra* in East Melanesia and the South-west Pacific is currently low (Zug 2013), with one very widespread form that shows evidence of regionally distinctive subpopulations (*Gehyra oceanica* (Lesson, 1830)), one moderately sized form from Palau (*Gehyra brevipalmata* (Peters, 1874)) and two very large species: *Gehyra vorax* Girard, 1858 from Fiji, and the recently described *Gehyra georgepottshaasti* Flecks, Schmitz, Böhme, Henkel and Ineich, 2012 from Vanuatu and the Loyalty Islands. A final taxon, *Gehyra mutilata* (Wiegmann, 1834) (or following Rocha *et al.* 2009 most likely *Gehyra insulensis* (Girard, 1858)) is also widespread, but may have been dispersed anthropogenically (Fisher 1997). Genetic data indicates additional lineages and endemic diversification of *Gehyra* within the Pacific, especially around the Solomon Islands and New Guinea (Tonione *et al.* 2016).

Until recently there has only been sporadic assessment of the herpetofauna of Manus and Mussau (Hediger 1933; Brown 1955), however recently several of the authors have independently undertaken surveys (RNF, SJR, JRC, PNT, MMTJ). This work has confirmed the presence of a large species of *Gehyra* on both islands. Genetic analyses indicate that the Manus and Mussau populations are conspecific, and that it is most closely related to (yet well divergent from) a clade of two species that occurs more than two thousand kilometres to the east in the south-west Pacific island groups of Vanuatu and Fiji. Two additional specimens of this species are also present in the Australian Museum, Sydney. Here we present a formal description of this new species, and discuss its biogeographic significance.

## Methods

**Genetics.** We sequenced five individuals of the new species in addition to one *Gehyra vorax* from Fiji and three *Gehyra georgepottshaasti* from Vanuatu (see Appendix 2 for full details of all specimens included in our genetic analyses) for an ~1000 base pair region of the mitochondrial ND2 gene using primers and protocols outlined in Sistrom *et al.* (2009). All new sequences are deposited in GenBank (Appendix 1). Sequences were aligned with and compared to molecular data taken from Sistrom *et al.* (2009) and Heinicke *et al.* (2011). Tamura-Nei genetic divergences (Tamura & Nei 1993) were estimated in MEGA v. 6 (Tamura *et al.* 2013).

We estimated phylogenetic relationships and timeframes of divergence using BEAST v 1.8.2 (Drummond & Rambaut 2007). These analyses largely used a dataset derived from sequences available in GenBank (comprising a single exemplar of recognized *Gehyra* species and major lineages), to which we added single exemplars of the new species, *Gehyra georgepottshaasti*, *Gehyra vorax* and the geographically most proximate population of *Gehyra membranacruralis* King and Horner, 1989 from northern New Guinea. To estimate divergence ages we used a secondary calibration strategy that is presented elsewhere (Oliver *et al.* 2016) that specifically focuses on two secondarily derived clade calibrations in *Gehyra*: firstly the divergence of Australian and Melanesian sister lineages 22 mya (SD 4.0), and secondly the radiation of Australian *Gehyra* 20 mya (SD 3.5). All analyses in

BEAST used the strict clock model, Yule speciation prior and GTR+G model of sequence evolution. We experimented with various strategies of data partitioning and what sequence data to include, but for the final analyses presented, we used an unpartitioned alignment with third positions removed to reduce the effect of saturation. Final analyses were run for 20 million generations and the first 20% of trees were discarded as burn-in, once it was confirmed that effective sample sizes were all above 200.

**Morphology.** Measurements of specimens were taken from the right side, to the nearest 0.1 mm using methods modified from Oliver *et al.* (2010) as follows: snout-vent length (SVL), trunk length from axilla to groin with limbs held at right angles (TrK), width of head at widest point (HW), head length from snout tip to anterior margin of tympanic opening (HL), depth of head at deepest point (HD), distance from posterior edge of nares to anteriormost edge of eye (EN), transverse distance between anterior and posterior extremities of exposed portion of the eye (IORB), post-mental scale length (POM), forearm length from base of palm to outer edge of elbow with limb strongly flexed (FA), crus length from base of heel to outer edge of knee with limb strongly flexed (CS), transverse eye diameter including surrounding ciliary scales (EYE), and transverse ear diameter (EAR). We also measured total post-vent tail length (TL) and regrown tail length with a ruler to the nearest 1 mm.

We counted internasals between the enlarged supranasals (IN), total number of enlarged (twice size of surrounding scales) supralabials (SUPR) to both midpoint of eye and to the inflection of mouth, enlarged infralabials to inflection of mouth (INFR), total number of expanded lamellae under fourth finger and fourth toe (including those not as wide as the toe) (LAMF4, LAMT4), and total number of pre-cloacal and femoral pores (POR) where they were present. We also scored whether folds were present on the anterior and posterior edge of the limbs, and along the lateral edge of the torso, following Flecks *et al.* (2012).

We examined comparative material from the Australian Museum (AMS), California Academy of Sciences (CAS), Museum of Comparative Zoology, Harvard University (MCZ), Museum of Vertebrate Zoology, UC Berkeley (MVZ), Museum Zoologicum Bogoriense, Indonesia (MZB), National Museum of Victoria (NMV), Northern Territory Museum and Art Gallery (NTM), Papua New Guinea National Museum (PNGNM), Royal Belgian Institute of Natural Sciences (RBINS), and South Australian Museum (SAMA). We also examined photographs of key types generously provided by staff from Naturalis, the Netherlands (RMNH) and the Museum Wiesbaden - Naturhistorische Sammlungen, Germany (MWNH).

## Results

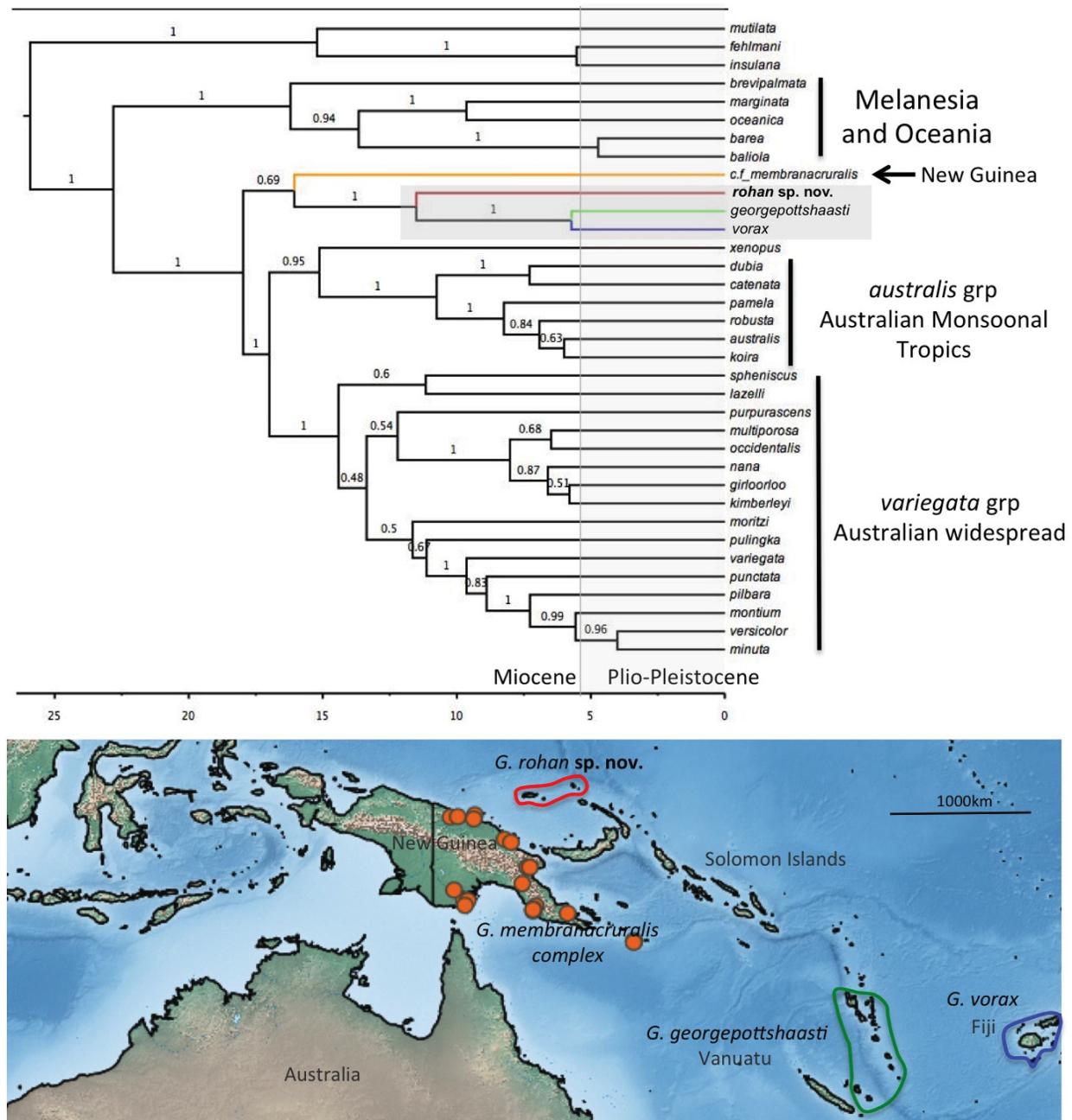
*Gehyra* sp. nov. from Manus and Mussau is deeply divergent from all congeners included in genetic analyses. Our alignment suggests that it is most closely allied to a lineage comprising the sister taxa *Gehyra vorax* from Fiji (mean Tamura-Nei distance 0.208) and *Gehyra georgepottshasti* from Vanuatu (mean Tamura-Nei distance 0.211). Samples of *Gehyra* sp. nov. from Mussau and Manus show low genetic divergence (Tamura-Nei distances 0.002–0.009).

Bayesian estimation of phylogeny also supports an association with *Gehyra* sp. nov. and a sister lineage comprising *G. georgepottshaasti* and *G. vorax* (posterior support of 1.0). A sister taxa relationship between the lineage containing these three taxa and another lineage of large sized and morphologically similar *Gehyra* from Papua New Guinea, *Gehyra membranacruralis*, was inferred but not strongly supported (Fig. 1).

Based on the secondary calibrations we used and focusing on the analyses in which potentially saturated 3rd codon positions of the ND2 gene were removed, Bayesian dating analyses suggest that the divergence of *Gehyra* sp. nov. from the lineage including the extant taxa *G. georgepottshaasti* and *G. vorax* occurred during the mid to late Miocene, and certainly before the beginning of the Pliocene (mean 11.6 million years ago (mya), 95% posterior distribution 7.1–15.9 mya). The divergence of this lineage of giant Pacific insular geckos from all other sampled *Gehyra* was even older, with divergence from the closest (albeit weakly supported) lineage of similarly large *Gehyra* in the *membranacruralis* group dating back well into the Miocene (16.1, 11.4–21.3 mya) (Fig. 1).

Examination and comparison of morphology revealed a suite of characters including body size, scalation and color pattern that diagnosed *Gehyra* sp. nov. from other recognized species of *Gehyra*, including closest relatives from Fiji and Vanuatu. Of particular importance, *Gehyra* sp. nov. differs from the types of *G. membranacruralis*, other specimens of this species from around the type locality in southern New Guinea (a region not genotyped in this study), and all other specimens tentatively referred to taxon from across New Guinea (Fig. 1) in its larger size

(adult SVL mean 138.4 mm (range 131.1–150.0) *versus* 119.8 mm (108.0–131.0)), in having heterogeneous dorsal scalation of larger scales bordered by distinctly smaller scales (*versus* comparatively homogenous) and in having a distinct orange eye ring in life (*versus* absent) (SJR pers obs.). Further diagnostic characters and specific comparisons are given in the diagnosis and comparisons sections below.



**FIGURE 1.** A) Phylogeny and timescale for diversification for *Gehyra* species estimated from first and second sites of the ND2 gene using BEAST (timescale in millions of years). Bayesian Posterior support values are given at nodes. Large bodied taxa from the Pacific and Melanesia are highlighted. B) Known distribution of four species of giant *Gehyra* in the south-west Pacific and Melanesian region.

## Systematics

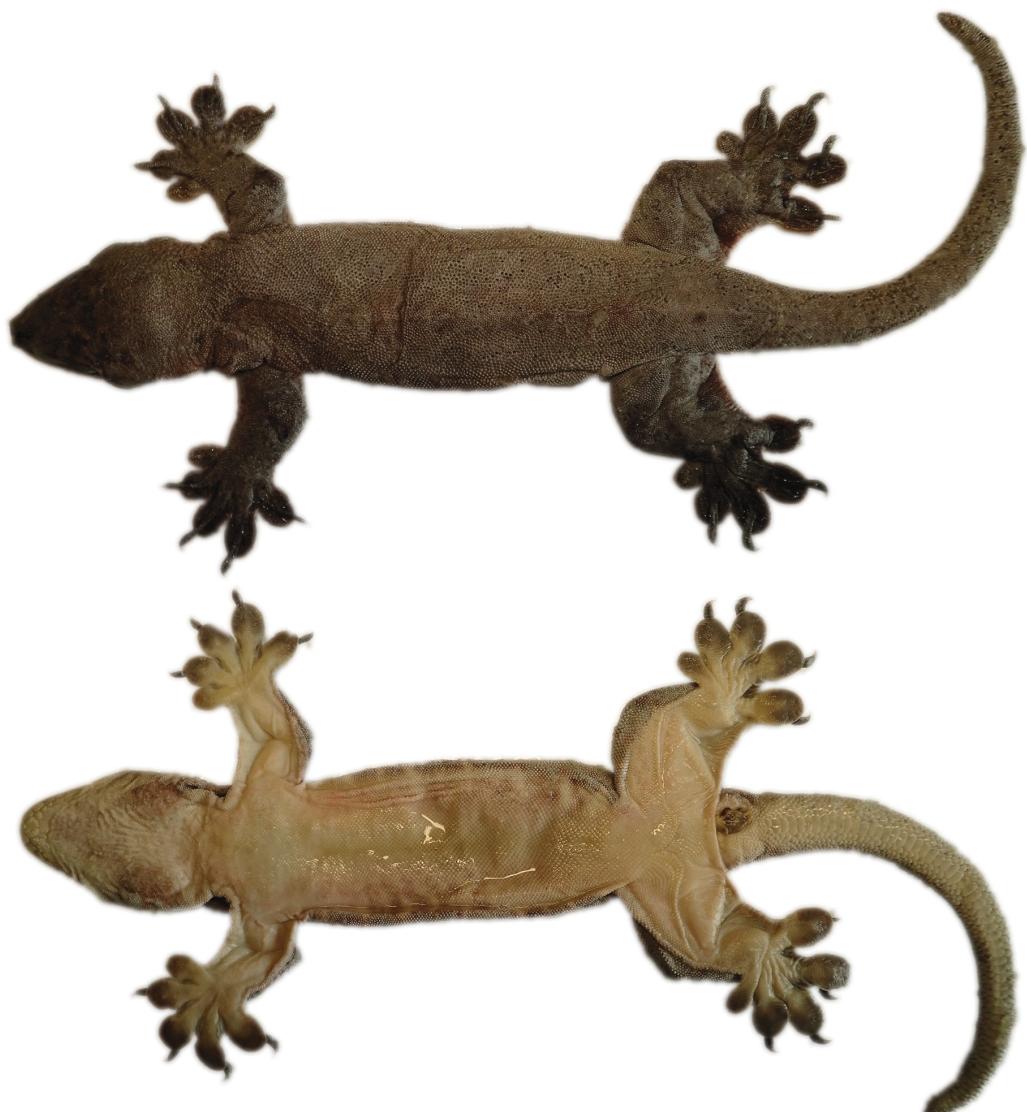
### *Gehyra* Gray, 1834

#### *Gehyra rohan* sp. nov.

Figs 2–5

**Holotype.** RBINS 2684 (Field No. PNG14-88), adult male, near Lorengau, Manus Island, Papua New Guinea (2.0388S, 147.2371E), collected 3 December 2014 by J. R. Clegg, P. N. Taylor and M. M. T. Jocque.

**Paratypes.** AMS R129497–129498, adult females, Lombrum, Los Negros Island, Admiralty Islands, Papua New Guinea (2.01S, 147.42E), collected 15 December 1951 by N. C. Goddard; CAS 252881, adult female, south bank of Lorengau River, 2.5 km southwest of Lorengau, Manus Island, Papua New Guinea (2.0415S, 147.2594E), collected 30 May 2010 by R. Fisher; PNGNM 25220 (PNG14-158), adult female, Yiringou Village, Manus Island, Papua New Guinea (2.0833S, 147.1167E), collected 9 December 2014 by J. R. Clegg, P. N. Taylor and M. M. T. Jocque; RBINS 2685 (PNG14-157), adult male, Yiringou Village, Manus Island, Papua New Guinea (2.0833S, 147.1167E), collected 9 December 2014 by J. R. Clegg, P. N. Taylor and M. M. T. Jocque; SAMA R69881 (SJR15105), adult male, near Nae, Mussau Island, Papua New Guinea (1.524S, 149.739E), collected 18 October 2015 by K. Aplin.



**FIGURE 2.** Preserved holotype of *Gehyra rohan* sp. nov. (RBINS 2684): A) dorsal view; and B) ventral view. Scale bar = 20 mm. Note diagnostic skin folds on the fore and hindlimbs, and widened subcudal scale row.

**Diagnosis.** *Gehyra rohan* sp. nov. is distinguished from other *Gehyra* species by the following suite of characters: very large size (adult SVL 130–150 mm), large head (HW/SVL 0.18–0.22, HD/SVL 0.11–0.14), prominent skinfolds on the anterior forelimbs and posterior hind limbs, weak lateral fold, heterogeneous dorsal scalation consisting of large rounded scales bordered by numerous much smaller rounded or triangular scales, massive digital discs with high number of wide undivided subdigital lamellae (finger IV 23–25, toe IV 22–26) that are not deeply notched or divided, rostral with near horizontal dorsal edge and not deeply notched, precloacal and femoral pores in a moderately long single continuous chevron of up to at least 40 pores, original tail without lateral serrations, slightly compressed and with a prominent medial row of enlarged subcaudals, and a prominent ring of orange scales around the eye in life.

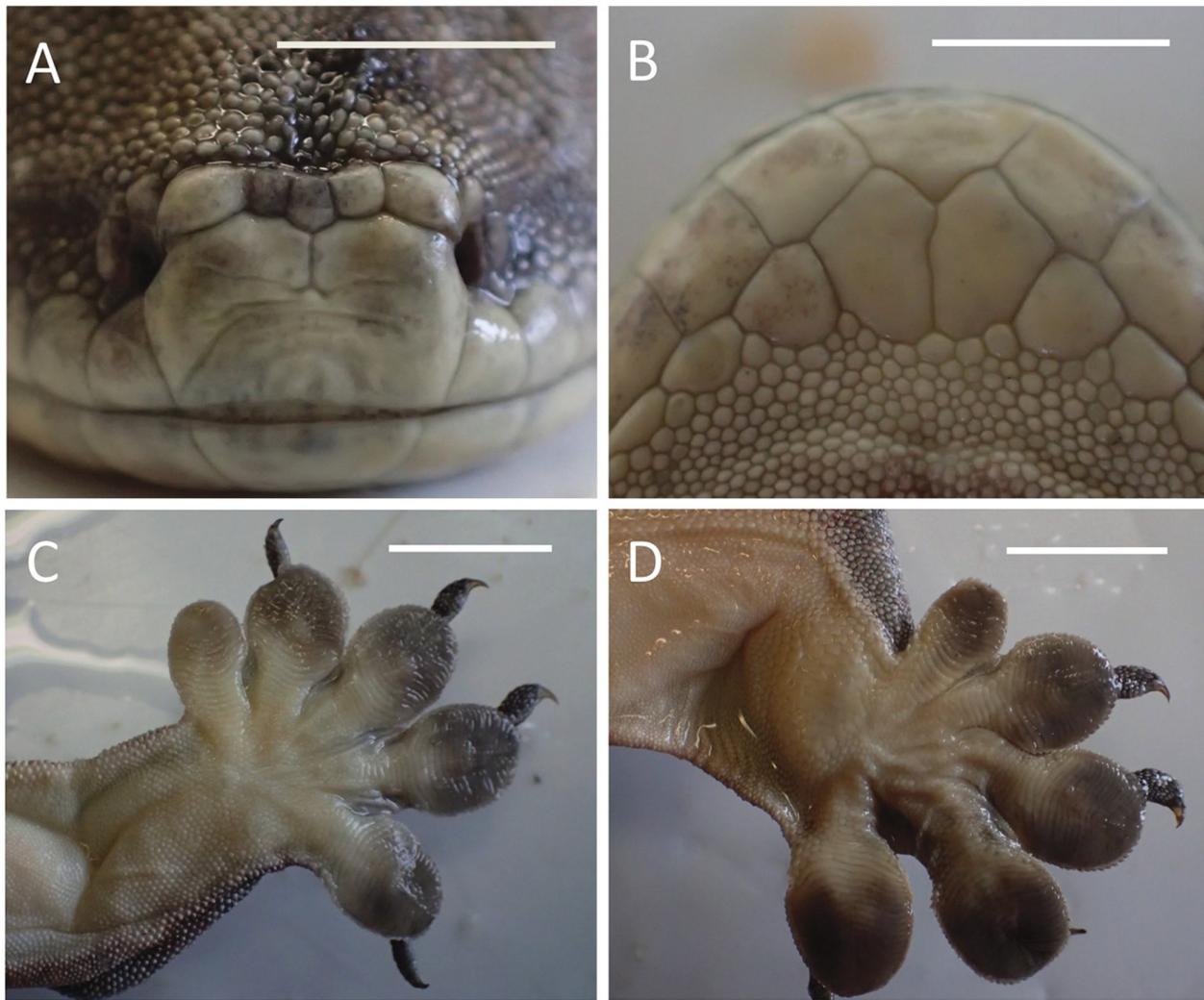
**Description of holotype.** Adult male. Habitus, large (SVL 140.3 mm) and robust (Fig. 2). Head triangular, robust (HW/HL 0.87), moderately long (HL/SVL = 0.23) and deep (HD/HL = 0.47). Snout long and robust (EN/HL = 0.35). Rostral large, broadly rectangular with rounded corners, rostral groove descends approximately 35% of rostral height, bifurcates, and extends to almost contact both nares (Fig. 3). Supranasals ovoid but with distinct points at ventrolateral edges, separated by three much smaller asymmetrical (becoming smaller from right to left) squarish internasals in a transverse series. Nares bordered by rostral, first supralabial, one large supranasal and three or four postnasals. Supralabials large and squarish with rounded dorsal edges, total number to inflection of mouth 14 (left) and 13 (right), and total number to midpoint of eye 11 (both sides). Supralabials bordered dorsally by 2–3 rows of enlarged scales. Infralabials large and squarish, total number to rictus of jaw 14 on both sides. Mental triangular, bordered by two infralabials and two large rounded postmentals (Fig. 3). Scales on dorsal surface of head tiny, irregular and slightly conical, becoming larger and flatter laterally and anteriorly. Superciliaries forming a brillar fold of small spiniform scales extending along the dorsal border of the orbit from anteroventral to posterodorsal corners. Pupil partially dilated, somewhat elliptical with limited crenulations.

Body robust (TrK/SVL 0.50). Dorsal and lateral scales distinctly heterogeneous in both shape and size, generally consisting of irregularly arranged large rounded scales, bordered by numerous much smaller rounded or triangular scales, often forming a ‘Star of David’ pattern; scales on nape much smaller than those on snout and torso. Ventral scales imbricate, arranged more regularly than those on dorsum, larger towards middle and posterior of venter, and tiny and granular on throat. Skin along ventrolateral edge of body loose and forming a weak fold along axilla-groin interval (Fig. 4). Precloacal and femoral pores (n = 40) arranged in a single recurved series terminating halfway along each femur. Hemipenal bulge present, moderately pronounced.

Limbs robust and fleshy, with prominent lateral folds along anterior and posterior edge of forelimb, posterior edge of hindlimb, and less prominently on anterior edge of hindlimb (Fig. 4). Digits on both the fore- and hind limbs with prominent and expanded pads; terminal phalanges free and with well developed claws on all digits except finger I and toe I. Subdigital lamellae undivided, wide under expanded portion of disk, tapering and becoming narrower than toe proximal to the expanded disc (Fig. 3); total lamellar counts for all digits as follows (left/right): fingers I = 23/23, II = 24/25, III = 26/26, IV = 30/31, V = 27/26; toes I = 21/19, II = 24/26, III = 28/28, IV = 32/27, V = 24/22; total number of lamellae under expanded portion of the disk (left/right): fingers I = 22/21, II = 18/21, III = 19/19, IV = 21/24, V = 21/22; toes I = 21/19, II = 20/21, III = 22/23, IV = 23/23, V = 23/22. Webbing extending to base of disc on all digits, folded in preservative.

Tail original, thin and short (107.8 mm in length) with blunt tip, much narrower than body at base; dorsal and lateral caudal scales granular and arranged irregularly, similar to dorsal scales on body; subcaudal scales distinctly enlarged, rounded, with a single medial row of 54 dilated (0.35–0.50 width of tail) ovoid scales extending full length of tail.

**Coloration in preservative.** Dorsal and lateral surfaces grey with an indistinct chestnut wash and scattered darker grey maculations, generally corresponding to a single scale. Dorsal surfaces of limbs with coloration similar to dorsum of body, becoming distinctly darker distally and on posterior skinfolds of hindlimbs. Ventral surfaces of body, limbs and tail predominantly plain light tan. Paired pinkish-brown regions on anterior lateral edges of throat, and also forming two series of faint bars extending along lateral edges of venter, from posterior edge of insertion of the forelimbs to anterior edge of insertion of hindlimbs. Subdigital lamellae under expanded discs of all digits beige proximally, tending distinctly darker greyish-brown distally. Tail coloration as for body, but with more dense dark grey maculations on dorsal surfaces.

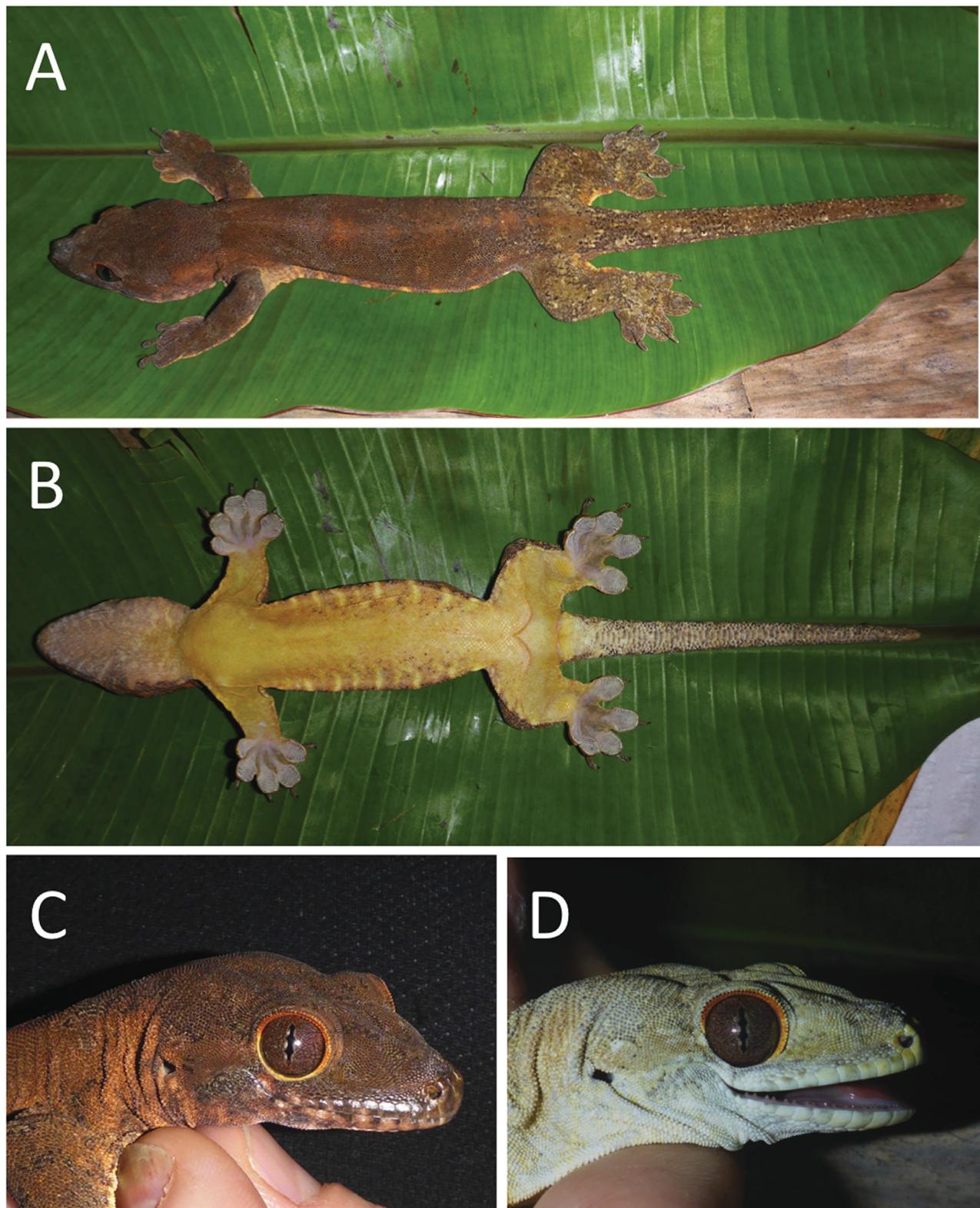


**FIGURE 3.** Details of holotype of *Gehyra rohan* sp. nov. (RBINS 2684): A) rostral configuration, scale = 5 mm; B) mental configuration, scale = 5 mm; C) subdigital lamellae hand, scale = 10 mm; and D) subdigital lamellae feet, scale = 10 mm.

**Coloration in life.** When initially captured: dorsal and lateral surfaces of head, body, limbs and tail dark chestnut brown mottled with patches of orange, light brown and off white, and with extensive black maculations, especially towards posterior region of dorsum and tail (Fig. 4). After capture: base dorsal color faded towards greyish but with same basic pattern (Fig. 4). Ventral surfaces of torso and limbs yellow, brightest anteriorly, undersurface of head brownish and digits white, transition between white of digits and yellow coloration of limbs relatively sharply defined, throat and torso both with regions of diffuse brown barring. Ventral surface of tail yellowish white with extensive dark-brown flecks. Scales around orbit forming a distinct orange ring, larger spiniform superciliary scales around dorsal edge bright reddish orange, grading to paler orange on smaller scales around ventral edge of eye.

**Details of holotype.** Measurements (in mm): SVL 140.3; TL 107.8; TrK 69.8; HW 27.5; HL 31.6; HD 14.8; EN 11; EYE 6.5; IORB 12.4; POM 3.4; FA 16.9; CS 18.8. Meristic data: IN 3; SUPR 14; INFR 14; LAMF4 23; LAMT4 25; POR 40.

**Variation.** Summary meristic values for all adults (2 males, 4 females) in the type series are as follows (mean, with the range in parentheses): SVL 138.4 (131.1–150.0); TL 107.2 (93.0–141.0); TrK 64.9 (58.0–72.6); HW 26.9 (24.5–29.8); HL 32.0 (30.2–35.0); HD 16.3 (14.8–18.80); EN 11.5 (10.9–13.2); EYE 7.6 (6.5–9.6); IORB 12.5 (11.4–13.7); POM 3.4 (3.0–3.8); FA 16.5 (15.5–17.3); CS 20.0 (17.7–22.7). Summary scalation information for these same 6 individuals are as follows: SUPR (to midpoint of eye) 10.5 (9–11); SUPR (rictus of mouth) 13.9 (12–14); INFR 12.7 (11–14); LAMF4 22.9 (21–25); LAMT4 24.1 (22–26); POR 36.5 (33–40).



**FIGURE 4.** Details of coloration on holotype *Gehyra rohan* sp. nov. (RBINS 2684): A) dorsum; B) venter; C) lateral view of head at time of capture; and D) lateral view of head after capture. All photographs by M. M. T. Jocque.



**FIGURE 5.** *Gehyra rohan* sp. nov. in life: A) holotype, RBINS 2684, near Lorengau Village, Manus Island, Papua New Guinea; and B) SAMA R69881 (SJR15105) near Nae, Mussau Island, Papua New Guinea. Photographs by M. M. T. Jocque and S. Venter.

The single male paratype SAMA R69881 (SJR15105) (Fig. 5) has a presumed developmental anomaly in which the pore-bearing and surrounding large scales have been shifted to the left, such that the right end of the pore series starts in the precloacal region, and extends almost fully along the left tibia, while the ventral scales on the right tibia are heterogeneous and do not appear to have formed properly. This specimen has two large, well-developed testes and in other respects appears to be a normal adult male.

All adult specimens are similar to the holotype and share the key diagnostic traits including a bright orange ring extending around the eye, wide subcaudals under the original tail and prominent skinfolds on the arms and legs, although the prominence of the latter character varies with the angle of limb preservation. Smaller specimens tend to have a plainer ventral coloration and less obvious brown barring and mottling on the throat and ventrum in preservative, suggesting that this pattern is most pronounced in adult specimens. The largest specimens in the type series are all female (max SVL 150 *versus* maximum of 140 mm for the males), raising the possibility that the species is sexually dimorphic like several other Pacific *Gehyra* (Zug 2013), but given the very small number of males, more material is needed to confirm this.

Based on photographs and field notes the dorsal coloration in life varies from quite dark chestnut brown to light grey, and the pattern of extensive but indistinct orange, greyish and brown mottling also varies in intensity. However much of this variation appears to be temporal, and single specimens vary extensively in appearance over short timescales (several hours) (Fig. 4).

**Comparisons.** Only four other species of *Gehyra* approach the large size (adult SVL consistently > 120 mm) of *Gehyra rohan sp. nov.*: *G. georgepottshaasti* (Vanuatu), *Gehyra marginata* Boulenger, 1887 (Maluku), *G. membranacruralis* (Papua New Guinea) and *G. vorax* (Fiji). Based on published descriptions (Flecks et al. 2012) and field observations (RNF, SJR and Fred Kraus pers. com.) these taxa all lack a complete, bright orange ring around the eye in life, although occasional specimens of *Gehyra vorax* do have a yellow contour (as opposed to orange) around the dorsal edge of the eye (RNF pers. obs., for an example see page 172 in Ryan 1998). *Gehyra rohan sp. nov.* further differs from *Gehyra marginata* in having enlarged subcaudals under the original tail (*versus* absent), in having a chestnut brown iris (*versus* light green), and in having a less prominent ventrolateral dermal fringe on the body; from *G. georgepottshaasti* in having rounded postmentals (*versus* distinctly elongate) (Flecks et al. 2012); from *Gehyra vorax* in having a lower number of femoral pores in adult males (up to 40 *versus* 58–90) (Beckon 1992); and from *Gehyra membranacruralis* by its heterogeneous dorsal scalation consisting of large rounded scales separated by numerous much smaller rounded or triangular scales (*versus* large rounded scales only), and by having larger enlarged subcaudals (maximum anteroposterior length on adults > 2.5 mm *versus* < 2.5 mm).

All other *Gehyra* are consistently smaller than *Gehyra rohan sp. nov.* *Gehyra baliola* (Duméril, 1851) and *Gehyra barea* Kopstein, 1926 from New Guinea and surrounding islands are moderately large (max SVL up to at least 105 mm), but *Gehyra rohan sp. nov.* can be readily distinguished from these taxa by the presence of prominent popliteal folds on the forelimbs (*versus* not prominent), a rostral that is not or barely notched, and low number of large internasals (*versus* rostral deeply notched (u-shaped) with a moderate to high number of very small granular internasals). *Gehyra serraticauda* Skipwith & Oliver 2014 is also large (potentially up to 120 mm SVL), but can be distinguished by the same characters as the preceding two species, in addition to having well-developed tail serrations (Skipwith & Oliver 2014).

The only congener recorded from Manus and Mussau is the widespread taxon *Gehyra oceanica*, from which *Gehyra rohan sp. nov.* is readily differentiated by its much larger adult size (> 100 mm *versus* < 100 mm), having enlarged subcaudals (*versus* absent), prominent popliteal skinfolds (*versus* absent), and distinctive orange ring around the eye in life (*versus* absent). The *Gehyra insulensis/mutilata* complex is also widespread in the Pacific, but *Gehyra rohan sp. nov.* is easily distinguished from this species complex by its much larger size (max SVL > 100 *versus* < 65 mm), and the absence of minute serrations along the lateral edges of the original tail (*versus* present).

**Distribution and ecology.** *Gehyra rohan sp. nov.* is recorded from several localities across Manus Island. While most type material is from the east, one author (SJR) observed a very large *Gehyra* that is most likely this species at in lowland rainforest at Yeri River (2.001S, 146.819E) in north-western Manus (Fig. 6). Older material has also been collected from nearby Los Negros Island (see paratypes). This species has also been recorded from a single site on Mussau Island. The extent of its distribution, if any, beyond these islands remains unknown. Beckon (1992) reported a large *Gehyra* supposedly from Nauna Island near Manus (UPNG 5772), but noted that as it was collected from a banana box so its ultimate provenance was uncertain. Based on morphology, especially its high number of pores (62) Beckon further suggested that this animal is consistent with specimens from Fiji. Given uncertainty about provenance and morphology at this stage do not consider this a confirmed record of *Gehyra rohan sp. nov.*

*Gehyra rohan sp. nov.* appears to be largely arboreal and is generally found in primary or disturbed lowland tropical rainforest (Fig. 6) on the trunks of large trees. It is also found on around human habitation in forested areas. Three of the authors (MJ, JRC, PT) found it to be reasonably common around Yiringou village in the interior of Manus, and two specimens were found on the same night on wooden beams below houses. The holotype was found running across a road in forest at night. The specimen from Mussau was found in a cave in disturbed forest close to the coast.

One paratype (CAS 252881), from forest on the bluffs above the Lorengau River, that was initially ~6 meters high on the trunk of a tree, “glided” approximately 3 meters to an adjacent tree trunk when disturbed. Similar gliding or parachuting behavior has been observed in *Gehyra mutilata* (Heyer & Pongsapipatana 1970), and in numerous other genera of arboreal lizards, including many that lack obvious adaptations for gliding (McGuire & Dudley 2011).

**Etymology.** Rohan is the Sohoniliu Village (Nali language) ‘tok ples’ (local language) name for this gecko. The community of Sohoniliu Village requested that this name be used for the formal description of this species, and we thank them for their support of this work.



**FIGURE 6.** Lowland Tropical Rainforest around the Yeri River in north-west Manus Island. A single specimen of *Gehyra rohan sp. nov.* was observed, but not collected on the trunk of a large tree partially obscured by vegetation on the left hand side of this photo. Photograph S. Richards.

## Discussion

**Endemism and Conservation in the Admiralty and St Matthias Islands.** The Admiralty and St Matthias Islands are recognized as hotspots of bird endemism (Stattersfield *et al.* 1998; Whitmore *et al.* 2015). The description of *Gehyra rohan sp. nov.* serves to highlight the growing number of endemics amongst other taxonomic groups. This includes frogs (four described species and several more undescribed), lizards (at least four or five endemic species) and terrestrial and volant mammals (two species recognised and several more unrecognised) (Zug & Fisher 2012, Richards *et al.* 2014, Timm *et al.* 2016, Tonione *et al.* 2016). Mussau is home to a smaller number of endemics,

including a frog, at least one lizard and potentially some bats (although several taxa again remain undescribed) (Whitmore *et al.* 2015; Weijola *et al.* 2016). This level of endemism exceeds that known from nearby and much larger New Ireland, and perhaps reflects a more stable and longer history of subaerial land in the Admiralty Islands.

A number of endemic species on Manus and Mussau appear to be threatened or very rare; in some cases this can be linked to the loss of primary forest (Weijola *et al.* 2016). In other cases such as the extinction of the small endemic bird, the Manus Fantail (*Rhipidura semirubra*) on the main island of Manus, the cause of decline remain uncertain (Whitmore *et al.* 2015). *Gehyra rohan sp. nov.* has only been detected once on Mussau, but is moderately common around human habitation in the interior of Manus Island, and is well known to local people. However, to date most records are in or close to primary forest, suggesting that (like other large *Gehyra* in the Pacific) it is arboreal and dependent on large trees (Beckon 1992), and may be vulnerable to primary forest loss. Although large areas of intact forest remain on Manus, much of the island is under logging concessions and further work is required to ensure the conservation of this and other endemic taxa.

**Ancient and recent biogeography of East Melanesia.** A growing number of molecular datasets are showing that the islands at the northern edge of the Australian plate (including both East Melanesia and island arcs that are now accreted into New Guinea) may have been accumulating genetically divergent endemic lineages since at least the late Miocene (Lucky & Sarnat 2010, Jönsson *et al.* 2011, Oliver 2011, Zug & Fisher 2012, Strickland *et al.* 2016). Both mitochondrial (presented here) and exon-based (Oliver *et al.* unpublished) genetic datasets indicate that *Gehyra rohan sp. nov.* is most closely related to a clade comprising *G. georgepotshaasti* from Vanuatu and *G. vorax* from Fiji. Estimates of divergence dates between *Gehyra rohan sp. nov.* and its relatives in Fiji and Vanuatu suggest that this clade has been present in East Melanesia or the south-west Pacific since the late Miocene, at a minimum. Most strikingly, these ages pre-date some estimates for the emergence time of current landmasses in the Admiralties, Vanuatu and Fiji (e.g. Davies *et al.* 2012). This argues for a long history in the region, although not necessarily on islands in their current arrangement.

The large apparent geographic disjunction (~2000 km) and deep Miocene divergences between *Gehyra rohan sp. nov.* and its nearest relatives in Vanuatu and Fiji is, as far as we can determine, a novel biogeographic pattern – at least amongst vertebrates. Previous and unpublished work on vertebrate lineages from the Admiralty Islands suggest much more recent origins and closer affinities to more proximate landmasses, either the New Guinea mainland (e.g bent-toed geckos *Cyrtodactylus*, Brown Tree Snakes *Boiga*, and cuscuses *Spilocuscus*) (Whitmore *et al.* 2015, Richmond *et al.* 2014, Paul Oliver unpublished) or other East Melanesian islands such as New Britain, New Ireland and the Solomons (e.g. Brown *et al.* 2015). While giant *Gehyra* tend to be highly arboreal and not regularly collected, it seems unlikely given the survey effort to date in the Solomon Islands and New Britain that they are present there but have gone completely undetected. The most plausible explanation for this disjunction is that the lineage pre-dates the uplift of these key intervening islands. There has however also been extensive extinction of Pacific vertebrates (Steadman 1999), and a potential role for both human mediated or naturally occurring biotic interactions in shaping this disjunction is difficult to test, but feasible. For example other very large geckos in the genus *Cyrtodactylus* appear to have more recently colonized the Solomon Islands from Milne Bay in New Guinea (Oliver *et al.* 2014, Worthington-Wilmer *et al.* 2016).

Finally, although Manus and Mussau are sometimes grouped together as a single area of endemism (Stattersfield *et al.* 1998), *Gehyra rohan sp. nov.* is actually one of the few endemics shared between both island groups (another is Meek's Pygmy Parrot *Micropsitta meeki*) (Mayr and Diamond 2001). Genetic samples of *Gehyra rohan sp. nov.* from Manus and Mussau are nearly identical, implying relatively recent overseas dispersal. This could have occurred via natural processes, however, an alternative is that the either the Manus or Mussau population has anthropogenic origins. It has also been suggested that the two species of pythons recorded on Mussau have anthropogenic origins (Schleip 2008, Whitmore *et al.* 2015). Similarly large *Gehyra* have been reported as a historically important food source in some areas of the Pacific (Gibbons and Clunie 1984, Beckon 1992), and Flecks *et al.* (2012) argued that very isolated records of *Gehyra georgepotshaasti* and *Gehyra vorax* in French Polynesia most likely had anthropogenic origins. More detailed sampling is required to test this hypothesis further. More broadly there remains much scope for further work to understand how geological change and prehistoric societies have shaped patterns of extinction and dispersal in the diverse south-west Pacific herpetofauna.

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## Literature cited

Beckon, W.N. (1992) The giant Pacific geckos of the genus *Gehyra*: morphological variation, distribution, and biogeography. *Copeia*, 1992, 443–460.  
<http://dx.doi.org/10.2307/1446204>

Boulenger, G.A. (1887) Remarks on Dr. A. Strauch's catalogue of geckos in the Zoological Museum of the Imperial Academy of St Petersburg. *Annals and Magazine of Natural History*, 5 (19), 383–388.  
<http://dx.doi.org/10.1080/00222938709460262>

Brown, W.C. (1955) A collection of lizards from Emirau Island (Saint Matthias Group). *The Silliman Journal*, 2, 87–92.

Brown, R.M., Siler, C.D., Richards, S.J., Diesmos, A.C. & Cannatella, D.C. (2015) Multilocus phylogeny and a new classification for Southeast Asian and Melanesian forest frogs (family Ceratobatrachidae). *Zoological Journal of the Linnean Society*, 174, 130–168.  
<http://dx.doi.org/10.1111/zoj.12232>

Cleere, N., Kratter, A.W., Steadman, D.W., Braun, M.J., Huddleston, C.J., Filardi, C.E. & Dutson, G. (2007) A new genus of frogmouth (Podargidae) from the Solomon Islands Results from a taxonomic review of *Podargus ocellatus inexpectatus* Hartert 1901. *Ibis*, 149, 271–286.  
<http://dx.doi.org/10.1111/j.1474-919X.2006.00626.x>

Davies, H.L. (2012) The geology of New Guinea — the cordilleran margin of the Australian continent. *Episodes*, 35, 87–102.

Doughty, P., Palmer, R., Sistrom, M.J., Bauer, A.M. & Donnellan, S.C. (2012) Two new species of *Gehyra* (Squamata: Gekkonidae) geckos from the north-west Kimberley region of Western Australia. *Records of the Western Australian Museum*, 27, 117–134.

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214–214.  
<http://dx.doi.org/10.1186/1471-2148-7-214>

Duméril, C. & Duméril, A. (1851) *Muséum d'Histoire Naturelle de Paris Catalogue méthodique de la collection des reptiles*. Gide et Baudry, Paris, 224 pp.

Fisher, R. (1997) Dispersal and evolution of the Pacific Basin gekkonid lizards *Gehyra oceanica* and *Gehyra mutilata*. *Evolution*, 51, 906–921.  
<http://dx.doi.org/10.2307/2411165>

Flecks, M., Schmitz, A., Böhme, W., Henkel, F.W. & Ineich, I. (2012) A new species of *Gehyra* Gray, 1834 (Squamata, Gekkonidae) from the Loyalty Islands and Vanuatu, and phylogenetic relationships in the genus *Gehyra* in Melanesia. *Zoosysterna*, 34, 203–221.  
<http://dx.doi.org/10.5252/z2012n2a1>

Gibbons, J.R.H. & Clunie, F. (1984) Brief notes on the voracious gecko, *Gehyra vorax*. *Domodomo*, 2, 34–36.

Girard, C. (1858) Descriptions of some new Reptiles, collected by the United States Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. Fourth Part.— Including the species of Saurians, exotic to North America, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 9, 195–199.

Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*, 20, 353–431.  
[http://dx.doi.org/10.1016/S1367-9120\(01\)00069-4](http://dx.doi.org/10.1016/S1367-9120(01)00069-4)

Hediger, H. (1933) Über die von Herrn Dr. A. Bühler auf der Admiralitäts-Gruppe und eingien benachbarten Inseln gesammelten Reptilien und Amphibien. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 44, 1–25.

Heinicke, M.P., Greenbaum, E., Jackman, T.R. & Bauer, A.M. (2011) Phylogeny of a trans-Wallacean radiation (Squamata, Gekkonidae, *Gehyra*) supports a single early colonization of Australia. *Zoologica Scripta*, 40, 584–602.  
<http://dx.doi.org/10.1111/j.1463-6409.2011.00495.x>

Heinicke, M.P., Greenbaum, E., Jackman, T.R. & Bauer, A.M. (2012) Evolution of gliding in Southeast Asian geckos and other vertebrates is temporally congruent with dipterocarp forest development. *Biology Letters*, 8, 994–997.  
<http://dx.doi.org/10.1098/rsbl.2012.0648>

Heyer, W.R. & Pongsapipatana, S. (1970) Gliding speeds of *Ptychozoon lionatum* (Reptilia: Gekkonidae) and *Chrysopela ornata* (Reptilia: Colubridae). *Herpetologica*, 26, 317–319.

Jönsson, K.A., Fabre, P.-H., Ricklefs, R.E. & Fjelds, J. (2011) Major global radiation of corvoid birds originated in the proto-Papuan archipelago. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 2328–2333.  
<http://dx.doi.org/10.1073/pnas.1018956108>

Kopstein, P.F. (1926) Reptilien von den Molukken und den benachbarten Inseln. *Zoologische Mededelingen*, 9, 71–112.

King, M. & Horner, P. (1989) Karyotypic evolution in *Gehyra* (Gekkonidae: Reptilia). V. A new species from Papua New Guinea and the distribution and morphometries of *Gehyra oceanica* (Lesson). *Beagle: Records of the Museums and Art Galleries of the Northern Territory*, 6, 169–178.

Kirch, P.V. & Catterall, C. (2001) The Mussau Islands: Natural and Cultural Environments. In: Kirch, P.V. (Ed.), *Lapita and Its Transformations in Near Oceania: Archaeological Investigations in the Mussau Islands, Papua New Guinea*. University of California, Berkeley, pp. 28–56.

Lesson, R.P. (1830) Description de quelques reptiles nouveaux ou peu connus. In: Duperrey, L.I. (Ed.), *Voyage Autour du Monde, Excut par Ordre du Roi, sur la Corvette de La Majest, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Zoologie*, Tome Second, 1<sup>re</sup> Partie. Arthur Bertrand, Paris, pp. 34–65. Plates 1–7.

Lucky, A. & Sarnat, E.M. (2010) Biogeography and diversification of the Pacific ant genus *Lordomyrma* Emery. *Journal of Biogeography*, 37, 624–634.  
<http://dx.doi.org/10.1111/j.1365-2699.2009.02242.x>

Mayr, E. & Diamond, J. (2001) *The birds of Northern Melanesia*. Oxford University Press, New York, 548 pp.

McGuire, J.A. & Dudley, R. (2011) The biology of gliding in flying lizards (genus *Draco*) and their fossil and extant analogs. *Integrative and Comparative Biology*, 51, 983–990.  
<http://dx.doi.org/10.1093/icb/icr090>

Oliver, P.M. (2011) Further evidence for old radiations originating at the northern edge of the Australian plate. *Proceedings of the National Academy of Sciences*, 108, E113.  
<http://dx.doi.org/10.1073/pnas.1104258108>

Oliver, P.M., Sistrom, M., Tjaturadi, B., Krey, K. & Richards, S. (2010) On the status and relationships of the gecko species *Gehyra barea* Kopstein 1926, with description of new specimens and a range extension. *Zootaxa*, 2354, 45–55.

Oliver, P.M., Sistrom, M. & Richards, S. (2012) Phylogeny and systematics of Melanesia's most diverse gecko lineage (*Cyrtodactylus*, Gekkonidae, Squamata). *Zoologica Scripta*, 41, 437–454.  
<http://dx.doi.org/10.1111/j.1463-6409.2012.00545.x>

Oliver, P.M., Skipwith, P. & Lee, M.S.Y. (2014) Crossing the line: increasing body size in a trans-Wallacean lizard radiation (*Cyrtodactylus*, Gekkota). *Biology Letters*, 10, 2014–2017.  
<http://dx.doi.org/10.1098/rsbl.2014.0479>

Oliver, P.M., Bourke, P., Pratt, R., Doughty, P. & Moritz, C.C. (2016) Systematics of the small *Gehyra* (Squamata: Gekkonidae) of the southern Kimberley, Western Australia: redescription of *Gehyra kimberleyi* Börner and Schüttler and description of a new restricted range species. *Zootaxa*, 4107 (1), 49–64.  
<http://dx.doi.org/10.11646/zootaxa.4107.1.2>

Oliver, P.M., Laver R.J., De Mello Martins, F., Pratt, R., Hunjan, S. & Moritz, C.C. (2016) A novel hotspot of vertebrate endemism and evolutionary refugia in the karstic Limestone Ranges of north-west Australia. *Diversity and Distributions*.  
<http://dx.doi.org/10.1111/ddi.12506>

Peters, W. (1875) Eine Mittheilung von Hrn. Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1874, 128–140.

Polhemus, D.A. (2007) Tectonic geology of Papua. In: Marshall, A.J. & Beehler, B.M. (Eds.), *The Ecology of Papua, Part I. The Ecology of Indonesia Series VI*. Periplus, Singapore, pp. 137–164.

Richards, S., Oliver, P. & Brown, R.M. (2014) A new scansorial species of *Platymantis* Günther, 1858 (Anura: Ceratobatrachidae) from Manus Island, Admiralty Archipelago, Papua New Guinea. In: Telnov, D. (Ed.), *Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea*. Entomological Society of Latvia, Riga, pp. 123–133.

Richmond, J.Q., Wood, D.A., Stanford, J.W. & Fisher, R.N. (2014) Testing for multiple invasion routes and source populations

for the invasive brown treesnake (*Boiga irregularis*) on Guam: implications for pest management. *Biological Invasions*, 17, 337–349.  
<http://dx.doi.org/10.1007/s10530-014-0733-y>

Rocha, S., Ineich, I. & Harris, D.J. (2009) Cryptic variation and recent bipolar range expansion within the Stumped-Toed Gecko *Gehyra mutilata* across Indian and Pacific Ocean islands. *Contributions to Zoology*, 78, 1–8.

Ryan, P.A. (2000) *Fiji's Natural Heritage*, 2<sup>nd</sup> edition. Exisle Publishing Company, New Zealand, 288 pp.

Schleip, W.D. (2008) Revision of the Genus *Leiopython* Hubrecht 1879 (Serpentes: Pythonidae) with the Redescription of Taxa Recently Described by Hoser (2000) and the Description of New Species. *Journal of Herpetology*, 42, 645–667.  
<http://dx.doi.org/10.1670/06-182R5.1>

Sistrom, M.J., Hutchinson, M.N., Hutchinson, R.G. & Donnellan, S.C. (2009) Molecular phylogeny of Australian *Gehyra* (Squamata: Gekkonidae) and taxonomic revision of *Gehyra variegata* in south-eastern Australia. *Zootaxa*, 2277, 14–32.

Sistrom, M., Donnellan, S.C. & Hutchinson, M.N. (2013) Delimiting species in recent radiations with low levels of morphological divergence: A case study in Australian *Gehyra* geckos. *Molecular Phylogenetics and Evolution*, 68, 135–143.  
<http://dx.doi.org/10.1016/j.ympev.2013.03.007>

Skinner, A., Hugall, A.F. & Hutchinson, M.N. (2011) Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography*, 38, 1044–1058.  
<http://dx.doi.org/10.1111/j.1365-2699.2010.02471.x>

Skipwith, P.L. & Oliver, P.M. (2014) A new *Gehyra* (Gekkonidae: Reptilia) from New Guinea with unique caudal scalation. *Zootaxa*, 3827, 57–66.  
<http://dx.doi.org/10.11646/zootaxa.3827.1.5>

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) *Endemic Bird Areas of the World. Priorities for Biodiversity Conservation*. Birdlife International, Cambridge, 846 pp.

Steadman, D.W., White J.P. & Allen, J. (1999) Prehistoric birds from New Ireland, Papua New Guinea: Extinctions on a large Melanesian island. *Proceedings of the National Academy of Sciences USA*, 96, 2563–2568.  
<http://dx.doi.org/10.1073/pnas.96.5.2563>

Strickland, J.L., Carter, S., Kraus, F. & Parkinson, C.L. (2016) Snake evolution in Melanesia: origin of the Hydrophiinae (Serpentes, Elapidae), and the evolutionary history of the enigmatic New Guinean elapid *Toxicocalamus*. *Zoological Journal of the Linnean Society*.  
<http://dx.doi.org/10.1111/zoj.12423>

Tamura, K. & Nei, M. (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, 10, 512–526.

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.  
<http://dx.doi.org/10.1093/molbev/mst197>

Thompson, J.E. (1952) *Report on the geology of Manus Island, TPNG with reference to the occurrence of bauxite*. Bureau of Mineral Resources, Australia, 11 pp.

Timm, R.M., Weijola, V., Aplin, K.P., Donnellan, S.C., Flannery, T.F., Thomson, V. & Pine, R.H. (2016) A new species of *Rattus* (Rodentia: Muridae) from Manus Island, Papua New Guinea. *Journal of Mammalogy*, 97, 861–878.  
<http://dx.doi.org/10.1093/jmammal/gyw034>

Tonione, M.A., Fisher, R.N., Zhu, C. & Moritz, C. (2016) Deep divergence and structure in the Tropical Oceanic Pacific: A multilocus phylogeography of a widespread gekkonid lizard (Squamata: Gekkonidae: *Gehyra oceanica*). *Journal of Biogeography*, 43, 268–278.  
<http://dx.doi.org/10.1111/jbi.12645>

Weijola, V., Donnellan, S.C. & Lindqvist, C. (2016) A new blue-tailed monitor lizard (Reptilia, Squamata, *Varanus*) of the *Varanus indicus* group from Mussau Island, Papua New Guinea. *ZooKeys*, 568, 129–154.  
<http://dx.doi.org/10.3897/zookeys.568.6872>

Whitmore, N., Aplin, K., Arihafa, A., Armstrong, K.N., Cuthbert, R., Müller, C.J., Novera, J., Richards, S.J., Tamarua, W., Theischinger, G. & Venter, F. (2015) *A rapid biodiversity survey of Papua New Guinea's Manus and Mussau Islands*. Wildlife Conservation Society Papua New Guinea Program, Goroka, Papua New Guinea, 85 pp.

Wiegmann, A.F.A. (1834) Beiträge zur Zoologie, gesammelt auf einer Reise um die Erde, von F. J. F. Meyen, M.D.A.D.N. Siebente Abhandlung. Amphibien. *Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae*, 17, 185–268.

Worthington-Wilmer, J. & Couper, P. (2016) Phylogeography of north eastern Australia's *Cyrtodactylus* radiation: a habitat switch highlights adaptive capacity at a generic level. *Australian Journal of Zoology*, 63, 398–410.  
<http://dx.doi.org/10.1071/ZO15051>

Zug, G.R. (2013) *Reptiles and amphibians of the Pacific Islands: a comprehensive guide*. University of California Press, Berkeley, 320 pp.

Zug, G.R. & Fisher, R.N. (2012) A preliminary assessment of the *Nactus pelagicus* species group (Squamata: Gekkonidae) in New Guinea and a new species from the Admiralty Islands. *Zootaxa*, 3257, 22–37.

**APPENDIX 1.** Genbank accession and tissue numbers for samples included in genetic analyses. Acronyms for specimens are as follows: ABTC Australian Biological Tissue Collection; AMS Australian Museum Sydney; LSU Louisiana State University; MZB Museum Zoologicum Bogoriense; RBINS Royal Belgian Institute of Natural Sciences; TG Tony Gamble collection; WAM Western Australian Museum; USNM US National Museum of Natural History.

*Gehyra australis* GQ257759 ABTC 28970; *Gehyra baliola* KJ025188 AMS R122405; *Gehyra barea* GU328677 ABTC 90224; *Gehyra brevipalmata* JN393910 USNM 559786; *Gehyra catenata* GQ257787 ABTC 77213; *Gehyra dubia* GQ257788 ABTC 76885; *Gehyra fehlmani* JN393948 TG 00723; *Gehyra georgepottshaasti* KX954307 LSU91233, KX954308 LSU91234, KX954306 TIS492; *Gehyra girloorloo* KX815518 WAM R113727; *Gehyra insulensis/mutilata* complex JN393951 AMS R132305; *Gehyra kimberleyi* KX815555 WAM R108747; *Gehyra koira* GQ257789 ABTC 30614; *Gehyra lazelli* GQ257807 ABTC 18031; *Gehyra marginata* JN393931 MZB lace 7666; *Gehyra membranacruralis* GQ257761 AMS R135529; *Gehyra minuta* GQ257753 ABTC 61706; *Gehyra montium* KX954309 WAM R132553; *Gehyra moritzi* KX954310 SAMA R65937; *Gehyra multiporosa* JX524085 WAM R171547; *Gehyra mutilata* GQ257762 ABTC 32321; *Gehyra nana* JN393920 AMS R140350; *Gehyra occidentalis* JX524094 WAM R172097; *Gehyra oceanica* JN393924 USNM 559790; *Gehyra pamela* KJ025205 ABTC 72525; *Gehyra pilbara* JX946973 WAM R165975; *Gehyra pulingka* KX954311 SAMA R42069; *Gehyra punctata* GQ257748 WAM R164116; *Gehyra purpurascens* KJ025302 ABTC 58138; *Gehyra robusta* JN393928 AMS NR2429; *Gehyra rohan* sp. nov. KX954303 SAMA R69881, KX954301 RBINS 2684, KX954300 RBINS 2685, KX954304 PNGNM 25220, KX954302 CAS 252881; *Gehyra spheniscus* KX954312 WAM R168715; *Gehyra variegata* KX954313 WAM R152913; *Gehyra versicolor* GQ257742 ABTC 41961; *Gehyra vorax* KX954305 RNF 9440; *Gehyra xenopus* GQ257790 ABTC 13017.

**APPENDIX 2.** Material examined for morphological comparisons. Institutional abbreviations are given in materials and methods.

*Gehyra barea*. RMNH 6625 (lectotype, largest specimen in series of three) Teon Island, South Banda Sea, Maluku Province, Indonesia; RMNH 5093 (paralectotype) Serua Island, south Banda Sea, Maluku Province, Indonesia; MZB lace 5438 (Field-number SJR 7719) 'Yakut Camp', Batanta Island, Papua Barat, Indonesia; MZB lace 5364 (Field-number SJR 7786) 'Waibya Camp', northern Salawati Island, Papua Barat, Indonesia.

*Gehyra baliola*. AMS R122399–122402, Fogamaiyu, Southern Highlands Province, PNG; AMS R122404, 122406, Waro, Southern Highlands Province, PNG; SAMA R64844, Gobe Ridge, Southern Highlands Province, PNG; CAS 121968–121969, Boze, Western Province, PNG; CAS 126667, 126671–126672 Matkomrae, Western Province, PNG; MCZ R139425, Emeti, Bamu River, Western Province, PNG; MCZ R22905, Merauke, Papua Province, Indonesia.

*Gehyra georgepottshaasti*. AMS R1158 'New Hebrides', [=Vanuatu]; NMV D02058–02059, D03244, Vanuatu.

*Gehyra lampei*. MWNH 690 (holotype), Bogadjim at Stephansort (German New Guinea), Madang Province, PNG.

*Gehyra marginata*. MZB lace 6062–6064, West Halmahera, North Maluku Province, Indonesia; MZB lace 38, Obi, North Maluku Province, Indonesia.

*Gehyra membranacruralis*. NTM R13746 (holotype), NTM R13744–13745 (paratypes), Port Moresby, PNG; USNM 518565, Tekedu, 11 km SW of Ivimka Camp, Gulf Province, PNG; MCZ R124129, Wipim, Western Province, PNG; MCZ 140719, MCZ R146026, Mawatta, Western Province, PNG; MCZ R135505, Waigani Swamp, National Capital District, PNG; MCZ R136092, Oriomo River, Western Province, PNG

*Gehyra insulensis/mutilata*. MVZ 268080, 268082, Tanah-Jampea Island, Sulawesi, Indonesia; MVZ 74897, 74900–74902, Morobe Province, PNG; MCZ R153056, Brown River, Central Province, PNG; MCZ R123256, Daru, Western Province, PNG.

*Gehyra oceanica*. SAMA R04920, SAMA R05178A–B, Kunua, Bougainville Province, PNG; SAMA R08224A–B, SAMA R08227A–C, SAMA R08231A–B, Mutahi, Bougainville Province, PNG; SAMA R08254, Topanas, Bougainville Province, PNG; SAMA R08686–08687, Keravat, East New Britain Province, PNG; SAMAR06728, Lagenda Plantation, Talasea, West New Britain Province, PNG; SAMA R06969, Kandrian, West New Britain Province, PNG; SAMA R60228–60229, Wanui Camp, East New Britain Province, PNG; SAMA R56833–56834, Barora Faa, Isabel Province, Solomon Islands; SAMA R56886, Kolopakisa, Isabel Province, Solomon Islands; SAMA R56957, Rob Roy Island, Choiseul Province, Solomon Islands; SAMA R57011, Tetepare Island, Western Province, Solomon Islands.

*Gehyra serraticauda*. MCZ R7314 (holotype), Fakfak, Onin Peninsula, West Papua Province, Indonesia.

*Gehyra vorax*. AMS R9515, Viti Levu, Fiji; AMS R 4768, Rewa River, Viti Levu, Fiji; CAS 159429, Navua, Viti Levu, Fiji; CAS 172616, 186243–186244, Namosi Province, Viti Levu, Fiji; CAS 186245, Verata, Tailevu, Viti Levu, Fiji.